Assessing the persistence capacity of communities facing natural disturbances on the basis of species response traits

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Abstract

Adequately assessing the ecosystem resilience and resistance is a challenging and essential question in the current context of widespread environmental change. Here we suggest the use of a quantitative measure we call Persistence Index (PI) to assess the capacity of communities to maintain their functions and services after disturbances. First, we present the formulation of PI that is based on the diversity, abundance, and redundancy of disturbance- and taxon-specific response traits. Then, we use simulated data sets to study the effects of species richness and the number and frequency of traits on PI values. Finally, we illustrate our approach by assessing the persistence capacity of forest communities in Peninsular Spain and the Balearic Islands in response to fire, drought and windstorm events. The Persistence Index was found to be relatively independent on the number of considered traits, but variable according to the frequency of traits in the community. In the evaluation made with national forest inventory data, PI was found to vary within and among different forest types, being particularly high in stands dominated by non-native species (e.g. *Eucalyptus* sp.) or in mixed-stands composed by evergreen and deciduous broadleaf species. We also found PI values to increase with the number of species present in the stand, although this relationship saturated due to overlap in species response traits. The presented index is complementary to other approaches developed to study the functional structure of communities through the distribution of species in a functional space. It can be applied to a broad spectrum of communities subjected to different types of stressors, making it a useful tool to guide ecosystem management decisions in a context of changing climate and uncertain disturbance regimes.

Key words

Response diversity, redundancy, disturbances, resilience, resistance

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1 Introduction

The management of natural resources has historically assumed environmental factors to remain relatively constant in time (Puettmann et al., 2013). However, this assumption is often no longer valid due to the increasing variability and uncertainty of driving forces, primarily climate (Lindner et al., 2010; Turner, 2010). Expected future changes in climatic conditions and socio-economic contexts lead to focus management efforts on preserving the ecosystems persistence and associated services (Allen et al., 2011; Folke et al., 2004; Gunderson, 2000; Oliver et al., 2015; Rist and Moen, 2013). According to Carpenter et al. (2001), assessing the persistence of ecosystems in the long-term requires to consider resilience and resistance as complementary concepts. Resilience is generally defined as the ability of ecosystems to undergo disturbance without shifting to an alternative state and losing its functions and controls (Gunderson, 2000), whereas resistance relates to the amount of external pressure needed to bring about a given amount of disturbance (Carpenter et al., 2001). Both concepts are considered essential to maintaining ecosystem functions, and they have been extensively developed (Brand and Jax, 2007; Lake, 2013). However, translating these concepts into practical operational indicators poses a major challenge since they are not easy to quantify (Lake, 2013; Rist and Moen, 2013).

The persistence of ecosystem properties and services can be approached through the assessment of the value, range and relative abundance of the species functional traits in a given ecosystem, understanding as functional traits those features of species considered relevant to their response to the environment (response traits) and/or their effects on the ecosystem functioning (effect traits) (see Diaz and Cabido, 2001; Díaz et al., 2007). This trait-based approach is gaining currency for resilience assessments of different ecosystems (Chillo et al., 2011; Kahiluoto et al., 2014; Laliberté et al., 2010; Oliver et al., 2015; Puettmann, 2011; Standish et al., 2014), and it ties into the insurance hypothesis, which posits that the greater the diversity of responses among species providing a given function, the lower the risk this function will be dramatically affected by changing events (Yachi and Loreau, 1999).

Up to now, several indices based on the range of species traits have been proposed to measure the components of functional diversity (FD) (i.e. functional richness, functional evenness, and functional divergence, *sensu* Mason et al., 2005). These indices aim at quantifying complementary characteristics of the distribution of species and their abundances in a multidimensional space whose axes represent functional traits (i.e. functional space *sensu* Mouillot et al., 2013). The more different the species in a community are, according to their traits, the higher FD values are and the higher the probability that a given ecosystem function is maintained. Accordingly, some FD indices have been suggested as good indicators to assess changes in community assembly processes along stress gradients (Mason et al., 2013; Mouchet et al., 2010; Mouillot et al., 2013).

In general, most of the FD approaches measure the range and diversity of trait values among the different species in a community (i.e. they appraise the presence of species with contrasted trait values). However, very few approaches have been developed based on the presence and abundance of specific traits that confer species with the ability to cope with changes (hereafter response traits). Some recent works have nevertheless proposed the use of response-and-effect frameworks in which relevant traits to the resistance and recovery of species are grouped according to functional groups (Neill and Puettmann, 2013; Puettmann, 2011) or related to the environmental variability (Sterk et al., 2013). Despite being promising methods to understand and assess ecosystem persistence to environmental variability and disturbances, neither provides a quantitative measure of the presence of certain trait values that are key to the ecosystem persistence.

Here we present a new index that can be used to assess the capacity of communities to maintain their functions when subjected to a given set of disturbances. We consider that ecosystem functions and services are potentially persistent when the species involved in their provision present traits that confer them resilience and/or resistance to their main stressors.

In the following, we first explain the rationale and calculation of the proposed Persistence Index (PI). We then use Monte Carlo simulations to illustrate its behavior under different conditions of trait frequencies and availability of trait information. To better understand the relationship between the PI and other indices, we compare PI values with other indices of taxonomic and functional diversity. Finally, to evaluate the performance of the index with real data, we apply our approach to tree communities across all forests in Peninsular Spain and the Balearic Islands. In particular, we assess how the PI is affected by species richness (i.e. the number of species) and how it varies within and across forest types. In the discussion, we show the main strengths and pitfalls of PI and discuss potential applications of the method.

2 The persistence index

2.1 Rationale of the index

The Persistence Index (PI) attempts to quantify the adaptive capacity of communities to disturbances. The index is based on the general assumption that an ecosystem will be more resilient and resistant to disturbances if it contains a greater presence of species with a given set of response traits (Elmqvist et al., 2003; Puettmann, 2011). PI integrates three different components related to the ecosystem persistence capacity: (*i*) the number of response traits present (Chillo et al., 2011; Elmqvist et al., 2003; Mori et al., 2013a; Newbery and Lingenfelder, 2009); (*ii*) the abundance of species presenting response traits, assuming that the more abundant these species are, the more likely the functions they provide to the ecosystem will persist after a disturbance; and (*iii*) the redundancy of response traits across species, which insures ecosystems against decline in their functioning thanks to the overlap in species response strategies (Yachi and Loreau, 1999).

2.2 Requirements and formulation

The design of PI is simple and flexible enough to be applicable to many kinds of communities, regardless of the set of species considered and the disturbances affecting them. To calculate PI in a particular target community, the required inputs are: (1) the set of species that are relevant for the persistence of the desired community state and/or function; (2) the main disturbances threatening the community's state and/or function; (3) the response traits that confer species with the ability to resist or recover from these disturbances; and (4) the abundance of species in the community. The method requires a species-specific response trait matrix $\mathbf{V} = \{v_{i,t}\}$, of dimensions $S \times M$, where the values of S species for M traits are stored. Values in $\mathbf{V}$ must be either quantitative or binary, although quantitative data need to be standardized to the [0, 1] interval prior to computing the index. It is also possible to use qualitative data if previously transformed into dummy binary variables, but missing values are not allowed (see Section 3.4 for an example of imputation). The index allows weighting response traits using a vector $\mathbf{w} = w_t$ (where w_t is the weight assigned to response trait t) for cases where not all response traits are considered equally relevant with respect to the set of disturbances under study. Finally, the method also

requires, for each target community, a vector $\mathbf{x} = x_i$ containing the relative abundance of the $i = 1, ..., S$ species. Species relative abundances are bounded between 0 and 1. They may be defined relative to the total abundance in the community (and hence be considered proportions and the sum is one) or relative to an arbitrarily fixed maximum abundance value (e.g. see definition of $\mathbf{x}$ in section 3.4). For the process of selecting the response traits, taxonomic levels other than species can be considered, but it is important to select traits with low variability within the considered taxon so as to avoid assigning incorrect trait values. For example, if we are considering species as the target taxonomic level, we should avoid response traits with high intraspecific variability.

PI is formulated as the product of two components, which we call *response trait richness* (RTR) and *response trait abundance* (RTA), and that are considered equally relevant to the persistence capacity of communities:

$$PI = RTR \cdot RTA \tag{1}$$

The product of the components allows obtaining high values of PI just when both RTR and RTA are relatively high, and penalizes its value when either RTR or RTA is low.

The response trait richness (RTR) component measures *the proportion of response traits present in the target community* with respect to the total number of traits selected as relevant to cope with the considered disturbances, and is calculated as:

$$RTR = \frac{\sum_{t=1}^{M} w_t \cdot max(v_{1,t}, ..., v_{S,t})}{\sum_{t=1}^{M} w_t} \tag{2}$$

where w_t is the weight assigned to response trait t and $v_{i,t}$ is the value of response trait t for species i.

The response trait abundance (RTA) component *measures the relative abundance in the target community of the selected response traits*, and is calculated as:

$$RTA = \frac{\sum_{t=1}^{M} \sum_{i=1}^{S} w_t \cdot v_{i,t} \cdot x_t}{\sum_{t=1}^{M} w_t} \tag{3}$$

where x_i is the relative abundance of species i.

Redundancy is indirectly considered in RTA since the inclusion of species sharing the same response traits as others already present in the community increases its value via the increase in the relative abundance of the traits.

Both components (RTR and RTA) range between 0 and 1, and consequently so does PI.

2.3 Simulation study

To illustrate the behavior of PI under different situations we used Monte Carlo simulations. We generated artificial communities for combinations of three factors: trait frequency, number of species (1 to 20), and number of traits (1 to 20). We considered three treatments of trait frequency distribution: (A) traits are unlikely to be present in most species; (B) traits have a probability of being present in species uniformly distributed between 0 and 1; and (C) traits are very likely to be present in most species. Presence/absence

values for response traits were generated by drawing from Bernoulli distributions in which the probability of trait presence was obtained using a beta distribution with parameters α and β depending on the trait-frequency treatment (Case A: $\alpha = 2$, $\beta = 10$; Case B: $\alpha = 1$, $\beta = 1$; Case C: $\alpha = 10$, $\beta = 2$) (see Fig. 1). Species abundances values were drawn from a uniform distribution and then standardized to relative abundances. For each experimental treatment (i.e. combination of trait frequency, number of species, and number of traits), we generated 10,000 replicate communities and calculated the value of PI (Fig. 1) and that of its components RTR and RTA (Appendix S3.1 of Supporting Information).

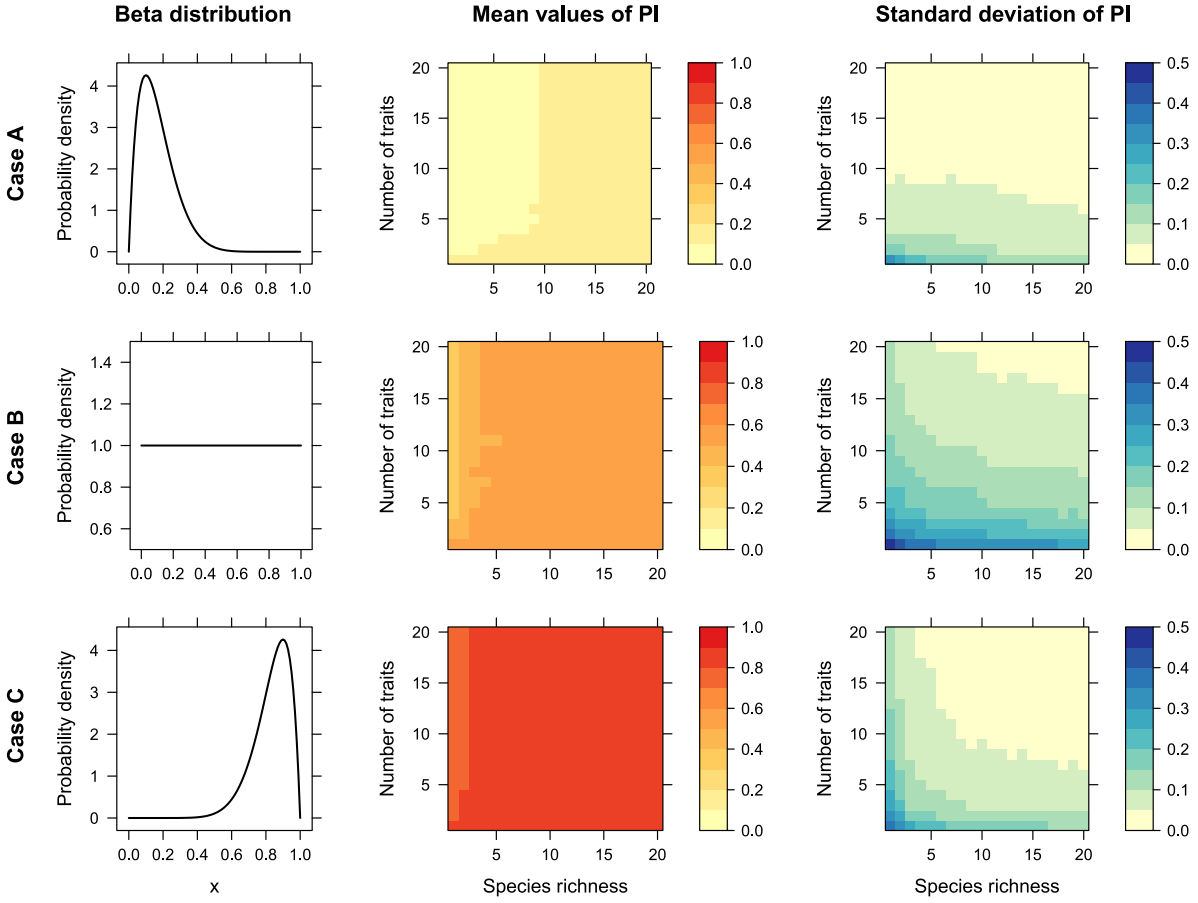

Figure 1: Mean and standard deviation values of PI calculated for MC simulated communities for combinations of three factors: trait frequency, species richness, and number of traits (see analogous figures for RTR and RTA in Appendix S3.1). Left panels show beta distributions used to define the probability of trait presence for each treatment of trait frequency (i.e. Cases A, B, and C).

We used communities corresponding to Case B (response traits being variably frequent in the community) with 10 response traits to compare our approach with other indices of taxonomic and functional diversity. Specifically, we calculated Pearson's correlation coefficients between PI, its components, and several common indices of taxonomic diversity (species richness [SR] and Shannon-Wiener diversity index [H']), and functional diversity (Functional Richness, Functional Evenness, Functional Divergence [FRic, FEve, and FDiv, Villéger et al. 2008], and Functional Dispersion [FDis, Laliberté and Legendre, 2010]). We adjusted significance values using Bonferroni corrections for multiple comparisons. All analyses were performed in R (R Development Core Team, 2014), and the "FD" package was used to calculate the FD diversity indices (Laliberté et al., 2014). We include an R function to calculate PI as supplementary

material (Appendix S3.2 of Supporting Information).

Central and right panels in Fig. 1 show the change in mean and standard deviation values of PI as a function of the number of species and traits considered, and for each of the three cases of trait frequencies described above. As expected, PI took the lowest values when the considered response traits were rarely present in the community, and increased with trait frequency. Regardless of the trait frequency, mean values of PI were found to be higher when less than five traits were considered in poor species-richness communities (central panels on Fig. 1). In these conditions the standard deviation also followed the same pattern, highlighting that the index is very dependent on the likelihood of such traits to be present in the species. This is particularly reflected in case B, where the higher variability of presence of traits compared to cases A and C leads to highly variable PI values (Fig. 1, right panels). Regarding species richness, PI value increased when species richness does. This effect, however, saturated at different richness values depending on the trait-frequency treatment (central panels on Fig. 1). When traits were unlikely to be present in the community (Case A), saturation occurred at a much higher value of species richness than when traits were very likely to be present (case C).

We found moderate Pearson correlations between taxonomic diversity measures and PI ($r = 0.47$ and 0.54 for SR and H', respectively), although correlations with RTR were stronger ($r = 0.65$ and 0.76 for SR and H', respectively) (Table 1). As expected, correlations between PI, RTR, RTA, and the FD indices were in general low or non-significant ($P > 0.05$). The strong correlation between RTR and FDis ($r = 0.79$, $P < 0.001$) is not surprising since both present similar mathematical formulation, although with different variables (i.e., representing different concepts).

Table 1: Pearson correlation coefficients between the Persistence Index (PI), its components (Response Trait Richness [RTR], and Response Trait Abundance [RTA]), species richness (SR), Shannon-Wiener diversity index (H'), functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis).

	RTR	RTA	SR	H	FRic	Feve	Fdiv	FDis
PI	0.85	0.71	0.47	0.54	0.30	NS	NS	0.54
RTR		0.26	0.65	0.76	0.50	NS	NS	0.79
RTA			NS	NS	NS	NS	NS	NS

3 Case study: The persistence index in the Iberian forests

3.1 Study area and data source

To evaluate the performance of the index in a real dataset, we calculated the PI for forest stands of all Peninsular Spain and the Balearic Islands, an area comprising a great variety of environments due to its contrasted topography, soil and climate conditions. Most of the study area (87%) belongs to the Mediterranean bioclimatic region, whereas approximately 11% falls within the Atlantic region and the remaining 2% to high-mountain areas belonging to the Alpine region (Ministerio de Agricultura Alimentación y Medio Ambiente, 2012). The area thus holds a wide range of plant species adapted to very different environmental conditions, being *Pinus* and *Quercus* the most abundant genera.

The western part of the Mediterranean region is considered one of the Europe's most change-vulnerable areas due to its location in a transition climatic zone (Giorgi and Lionello, 2008; Lavorel et al., 1998) and

the strong dependence of its landscapes on traditional rural activities, now mostly abandoned (Ameztegui et al., 2010; Farina et al., 2003; Otero et al., 2013; Sala et al., 2000). Currently, the occurrence of the main abiotic disturbances in the study area –wildfires, severe drought periods, and windstorm events (Allen et al., 2010; Giorgi and Lionello, 2008; Martín-Alcón et al., 2010; Pausas and Fernández-Muñoz, 2011; Schelhaas et al., 2003)– is expected to increase under future forecasted conditions (Allen et al., 2010; Lindner et al., 2010).

We used the Third Spanish National Forest Inventory (SNFI) as source of community data (Ministerio de Medio Ambiente 1997-2007). The SNFI was carried out following a systematic sampling design in which permanent circular plots were located at the intersections of a 1×1 km UTM grid that fell inside forest and other woodlands. Each plot is composed of four nested subplots in which trees are inventoried depending on their diameter at breast height (DBH) and distance to the plot center. Subplot sizes ranged from 5 m radius, where trees with a DBH lower than 12.5 cm were inventoried, to 25 m radius, for trees with DBH of at least 42.5 cm. We used a total of 74,581 forest plots distributed across the study area and including 136 taxa (species and genus) belonging to a total of 57 genera, 28 families and 20 orders (see Appendix S3.3 of Supporting Information). In order to ensure that some traits were not absent due to the immaturity of trees, we discarded trees with a DBH lower than 7.5 cm. Although shrubs are often abundant in Mediterranean forests and perform important functions for forest ecosystems (Eldridge et al., 2013), we did not consider shrub species in this case study as we lacked sharp information on some response traits for many of them. Despite the high overall number of tree species present in the study area, almost all plots (94.7%) contained three or less species, and nearly 60% qualified as monospecific.

We classified the SNFI plots into seven forest types according to their tree species composition and the different ecological functions they can perform: (1) pine forests; (2) evergreen-broadleaf; (3) deciduous-broadleaf; (4) mixed evergreen-deciduous broadleaf; (5) other conifer-forests; (6) forests of non-native species; and (7) other mixed forests (see Table S3.4.1 in Appendix S3.4 of Supporting Information for details on the criteria followed to classify the SNFI plots into forest types). According to this classification, more than one third of plots (37.2%) are in pine-dominated forests, whereas 19.2 and 17.5% of the plots correspond to forests dominated by evergreen-broadleaf and deciduous-broadleaf species, respectively.

3.2 Data preparation

We selected six macroscopic traits that have been reported to confer forest species resistance and/or resilience to drought, forest fires, and windthrow. We only chose traits with low or null intraspecific variation and for which information was available for most of the consulted species. The selected traits were: (1) hard and thick sclerophyllous leaves, which improve plant tolerance to drought (Lopez-Iglesias et al., 2014; Matesanz and Valladares, 2014); (2) long-lived seed banks and (3) traits related to disturbance-stimulated recruitments (such as serotiny or heat-shock-triggered germination), both considered adaptive traits in dry and fire-prone environments (Keeley et al., 2011; Nathan et al., 1999; Paula et al., 2009; Pausas et al., 2008); (4) high wood density, which is critical for coping with mechanical hazards associated to windthrow (Chave et al., 2009); and (5) resprouting ability and (6) rooting depth, which are associated to adaptation to various disturbance agents (Keeley et al., 2011; Lopez-Iglesias et al., 2014; Matesanz and Valladares, 2014; Nicoll et al., 2006; Nzunda et al., 2014; Pausas et al., 2008; Zeppel et al., 2014). Whenever information on one of the selected traits was unavailable for a given species, we used the average value of that trait for species of the same genus. With all the collected information, we generated a data table (i.e. matrix $\mathbf{V}$) in which presence or absence of each response trait was specified for each species, on

a binary basis, following the criteria defined in Table 2. For the few cases where the trait of a given genus was unknown, we conservatively set v_{it} to zero.

We defined the relative abundance of each species in each plot (x_i) assuming that the percentage value of forest cover in the whole stand (FC, %) was relevant for PI, so that the sum of x_i values had to be equal to ($FC/100$) instead of being equal to one. Specifically, we calculated x_i as:

$$x_i = \frac{N_i \cdot (FC/100)}{\sum_{i=1}^{S} N_i} \tag{4}$$

where N_i is number of trees of the species i per hectare.

To account for the different levels of relevance of the response traits considered, we assigned them weights (w_t) depending on the number of disturbances for which each trait may have a positive effect in species persistence. In an effort to decrease subjectivity in this assessment, weights were decided after consulting a group of twenty forest ecology experts following the Analytic Hierarchy Process (AHP) (Saaty, 1977). Table 2 shows the trait weights calculated based on the criteria of the consistent experts consulted in the AHP questionnaire (i.e. those in which Saaty's inconsistency was lower than 0.10).

3.3 Statistical analysis

We quantified and mapped PI for each SNFI plot in the study area. We also studied the relationship between species richness and PI, and compared mean PI values across forest types via ANOVA and a Tukey's HSD test. In order to assess the effect of assigning equal or different weights to each response trait, we calculated Pearson's correlation coefficient between PIs calculated taking weights obtained from the AHP (PI_{AHP}) and PIs calculated assuming that all response traits had the same weight (PI_{ew}). We also calculated Pearson's correlation coefficients between both components of PI (RTR and RTA) for each forest type. We adjusted significance values using Bonferroni corrections for multiple comparisons. All analyses were performed in R (R Development Core Team, 2014), and we used the "pmr" package to calculate weights through AHP (Lee and Yu, 2014).

3.4 Results and discussion of the case study

We found information on the selected response traits for almost all taxa (93.4%, Fig. 2). Among the 136 taxa considered, only seven (5.1%) simultaneously presented all the response traits, whereas 75% presented less than a half of the relevant response traits (i.e. three or less). Resprouting ability, deep roots and hard downy leaves were the most frequent traits, being found present in 74.3, 70.6 and 63.2% of the study taxa, respectively (Fig. 2). Broadly speaking, we obtained relatively low PI values in our study area (74.2% of plots presented a PI lower than 0.3, and only 4.5% of plots reached a PI higher than 0.5). Those areas with the lowest PI values were located in central mountain ranges, while plots with PI greater than 0.5 were mostly found in the northeast and northwest parts of the study area (Fig. 3). Many plots presented several response traits as a result of species adaptation to the main disturbances of the Mediterranean region (Matesanz and Valladares, 2014; Pausas et al., 2008; Valladares et al., 2004), and this was reflected in the RTR values, most of which were higher than 0.5 (0.67 ± 0.17; $mean \pm SD$) (Figs. 4 and 5). However, it was very common to find in our dataset plots with relatively low cover values (only 30% of them showed FC values above 70) or being dominated by species presenting very few

Table 2: Response traits used in the empirical calculation of the Persistence Index in the Iberian forests, including the disturbances for which the traits foster persistence, the criteria used to define whether a species presents the traits, the sources of information used to construct the response trait database (Appendix S3.3), and the weights assigned to each response trait in the Analytic Hierarchy Process.

Response trait	Associated disturbances	Criteria	Consulted sources	Weight (w_t)
Resprouting ability from roots or crown	Fire, wind, drought	Reference considerations	López González 2001, Ruiz de la Torre 2006, Serrada et al. 2008, Gómez-Manzanedo et al. 2009, Green 2009, Paula and Pausas 2009, Paula et al. 2009, Bagaria et al. 2012	0.361
Stimulated recruitment after disturbances	Fire, drought	Serotinous cones, heat-stimulated germination, quick post-disturbance emergence	Paula and Pausas 2009, Paula et al. 2009	0.214
Hard and downy leaves	Drought	Presence of hard and thick cuticle, downy leaf underside	López González 2001, Ruiz de la Torre 2006	0.175
Seed bank longevity	Drought, fire	Higher than 3 yrs, between 1 and 5 yrs, less than 4 yrs	Catalán Bachiller 1991, Kleyer et al. 2008, Paula and Pausas 2009, Paula et al. 2009	0.109
Rooting depth	Drought, wind	Roots deeper than 1.5 m, taproot systems	Lemoine et al. 2001, Crow 2005, Ruiz de la Torre 2006, Serrada et al. 2008, Green 2009, Nicolescu et al. 2009	0.105
Wood density	Wind	Higher than 0.601 $g \cdot cm^{-3}$	Rodríguez et al. 2006, Chave et al. 2009, Zanne et al. 2009, Vilches-Casals and Correal-Mòdol 2013	0.034

response-traits. This resulted in RTA values (and in turn the PI values) generally low (Figs. 4 and 5).

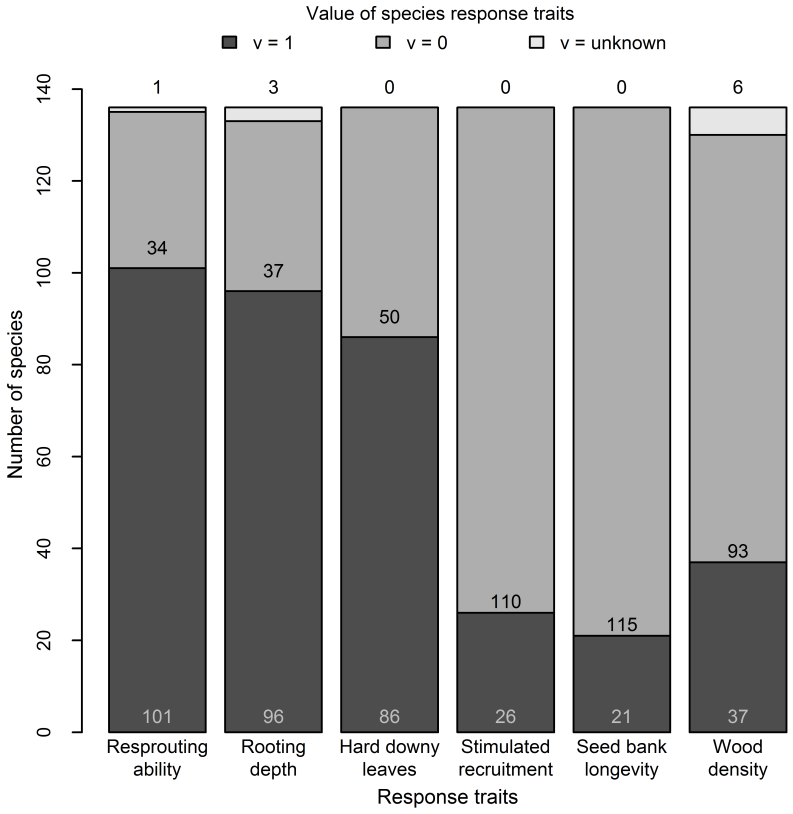

Figure 2: Number of species in the 3rd Spanish Forest National Inventory with presence (black) or absence (grey) of each considered response trait based on criteria defined in Table 2, and number of species for which information on the response trait was unavailable (light grey).

We observed a remarkable variability of PI values within each forest type (coefficient of variation ranging between 0.34 and 0.91). Considering all forest types together, the variability was wider for RTR (coefficient of variation between 0.10 and 0.45) than for RTA (coefficient of variation between 0.31 and 0.54). However, the variability of RTR was found to be lower than the one for RTA within forest types (Fig. 4). Although our analysis showed that both the RTR and RTA components of PI were positively and significantly correlated regardless of forest type, the values of the correlation were not high except for the ones composed by non-native species or by conifers different from pines.

Non-native forests presented the highest PI values (0.43 ± 0.25; Fig. 4). Most of these plant communities (61.3% of plots) include species of *Eucalyptus* (mostly *E. globulus* Labill.), a genus that is able to persist in the driest and most fire-prone regions in the world (Gill, 1975; Pekin et al., 2009) and is considered fire-resilient (Catry et al., 2013; Pekin et al., 2009). Note, however, that traits conferring resilience and resistance to disturbances may also favor invasiveness (Matesanz and Valladares, 2014), as in the case of some *Eucalyptus* species which have been reported to show invasive behavior in the Iberian Peninsula (Sanz-Elorza et al., 2001). Contrary to many Mediterranean broadleaf species, most conifers in our study area present very few response traits according to the criteria defined in this study. Accordingly, forests dominated by pines and other conifer species showed very low PI values (0.19 ± 0.08 and 0.11 ± 0.10, respectively; Fig. 4). Along these lines, other studies have previously found that conifer species show less resilience and resistance to fire and other disturbance agents than other typical Mediterranean species such

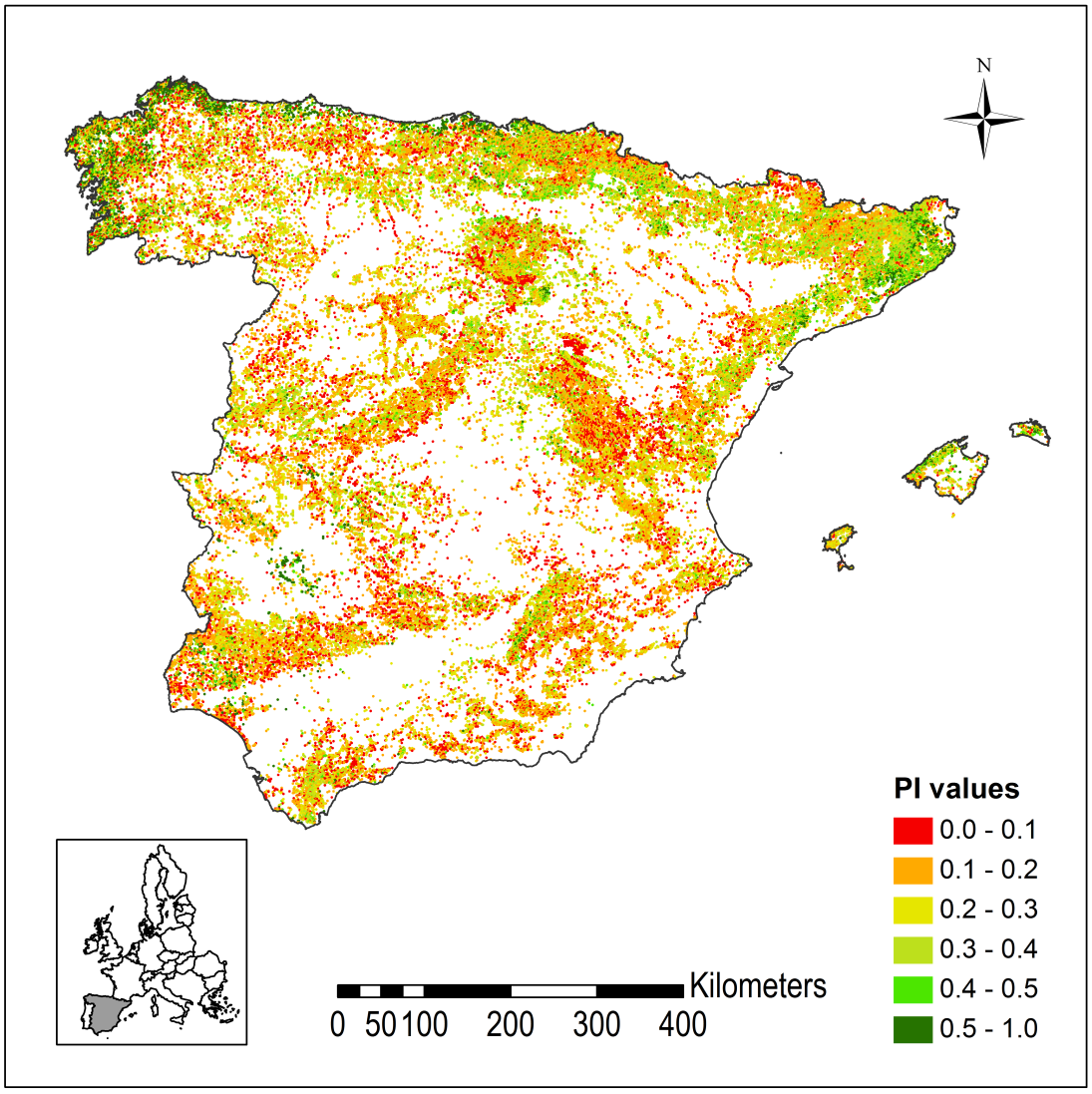

Figure 3: Distribution of plots according to determined PI values. Note that the categories are not uniform as the last one includes PI values greater than 0.5. Location of the study area in Europe is shown at the bottom left.

as *Quercus* (Hanewinkel et al., 2013; Pausas et al., 2008; Rodrigo et al., 2004). Mixed evergreen-deciduous broadleaf forests and other mixed forests were found to be among the most potentially persistent to change ($PI = 0.30 \pm 0.11$ and 0.35 ± 0.12, respectively; Fig. 4).

We observed that PI and RTR increased with species richness, but the effect saturated at richness values above three (Fig. 5), as already observed in the theoretic simulations (see central panels on Fig. 1). Previous studies have already shown that mixed forests with two or three species belonging to different functional groups (i.e. evergreen and deciduous species) are more resistant and resilient to disturbances than monospecific ones (Drobyshev et al., 2013; Knoke et al., 2008; Lebourgeois et al., 2013; Pretzsch et al., 2013). In this sense, Brang et al. (2014) recommend increasing tree species richness as a management strategy to enhance the adaptive capacity of forests in response to uncertainties linked to global change. Although plots with lower species richness presented the lowest mean PI values, they also counted the plots with the greatest absolute PI values. For example, PI values higher than 0.9 were only present in plots with four or less species, all of which had a high proportion of *Eucalyptus* and were classified as forests of non-native species. Indeed, this result was also expected from simulations, where low species richness led to higher variability in PI (see right panels on Fig. 1).

A strong and significant correlation ($r = 0.96$; $p - value < 0.001$) was found between PI calculated considering equal (PI_{ew}) and different (PI_{AHP}) weights of each response trait. Complementary analyses indicated that this behavior is a specific result of this case study and that the higher the differences between trait weights, the lower the correlations between PI for different weight schemes (not shown).

4 Discussion

4.1 Evaluating the Persistence Index

In the current context of global change it is essential to develop quantitative tools to gauge ecosystem resilience and resistance to natural disturbances (Carpenter et al., 2001). Such tools can be highly useful in the implementation of pre- and/or post-disturbance management decisions designed to ensure the sustainable future provision of desired ecosystem services (Oliver et al., 2015; Seidl et al., 2015). Here we present an approach that attempts to address this need based on the relevance that presence, abundance, and redundancy of macroscopic species response traits have in ecosystems resistance and resilience (Diaz and Cabido, 2001; Elmqvist et al., 2003).

The Persistence Index (PI) is easy to calculate and presents properties that make it applicable to different types of communities affected by any type of stressor. Both the species and the response traits included in the index calculation are defined *a priori* as a function of the particular set of ecological functions and disturbances considered. This characteristic allows specifying which system state and perturbations are of interest, a crucial aspect to make the resilience concept operational (i.e. *resilience of what to what*, Carpenter et al., 2001). The fact that all trait values are required to be standardized to the [0, 1] interval avoids biases due to different measurement units for each trait while enabling comparability between index values on ecosystems in different regions or subjected to different disturbance regimes. For example, in the particular case of forest communities, the PI can be used to compare the persistence of forests of southern Europe (mainly disturbed by drought and forest fires) against forests of central Europe (where windthrow and storm events are the main threats). Finally, this index also allows different weights to be assigned to each trait to enhance the flexibility and accuracy of its estimations. However, objectively

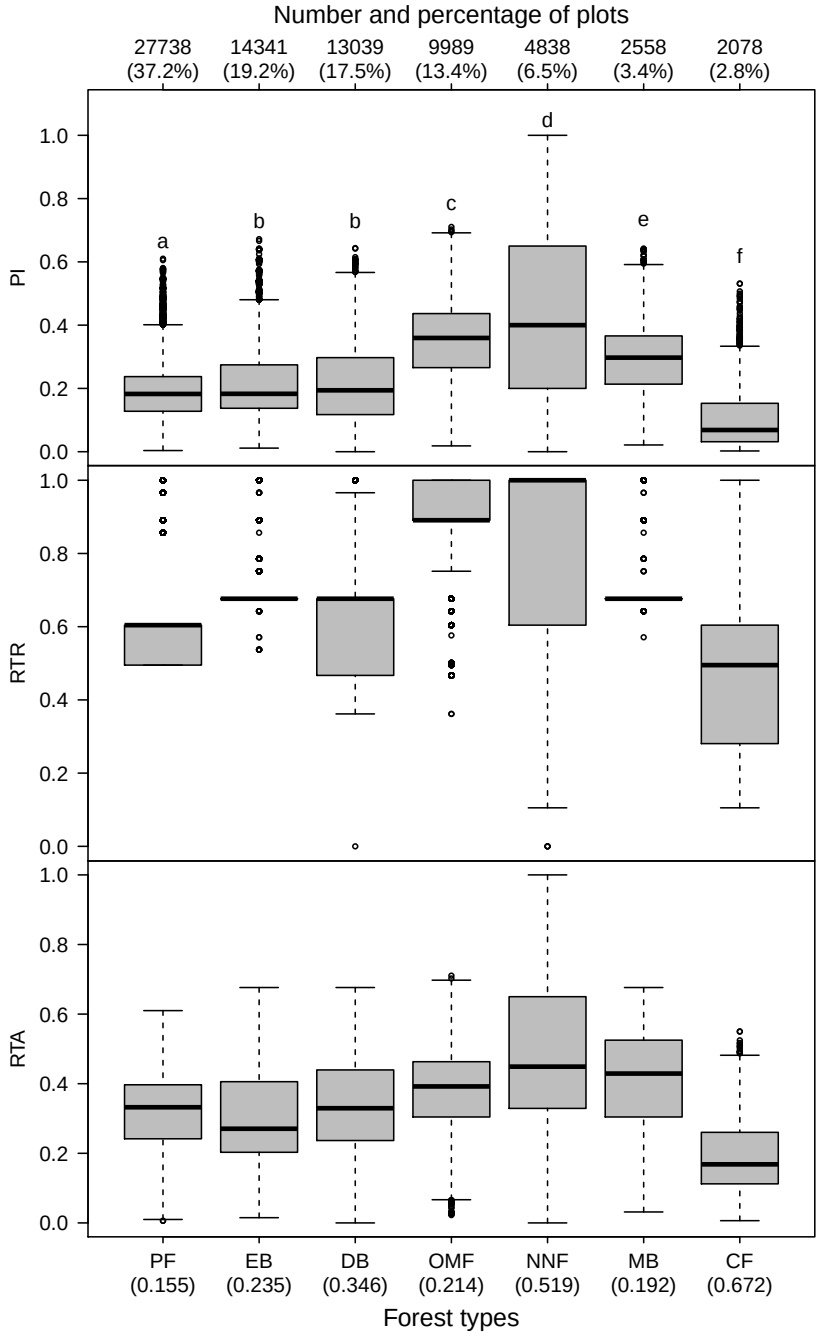

Figure 4: Distribution of PI (top), RTR (centre) and RTA (bottom) values for the main defined forest types in the study area.(PF: pine forests; EB: evergreen broadleaf forests; DB: deciduous broadleaf forests; NNF: forests of non-native species; MB: mixed evergreen-deciduous broadleaf forests; CF: other conifer forests; OMF: other mixed forests). Black lines in box centres are medians, boxes show interquartile range (25-75%) and whiskers show 1.5 interquartile range. Top axis shows total number and percentage of plots for each forest type in the study area. Bottom axis shows the Pearson's correlation coefficient between RTR and RTA for each forest type (in brackets). Letters in the top figure are based on Tukey's HSD test.

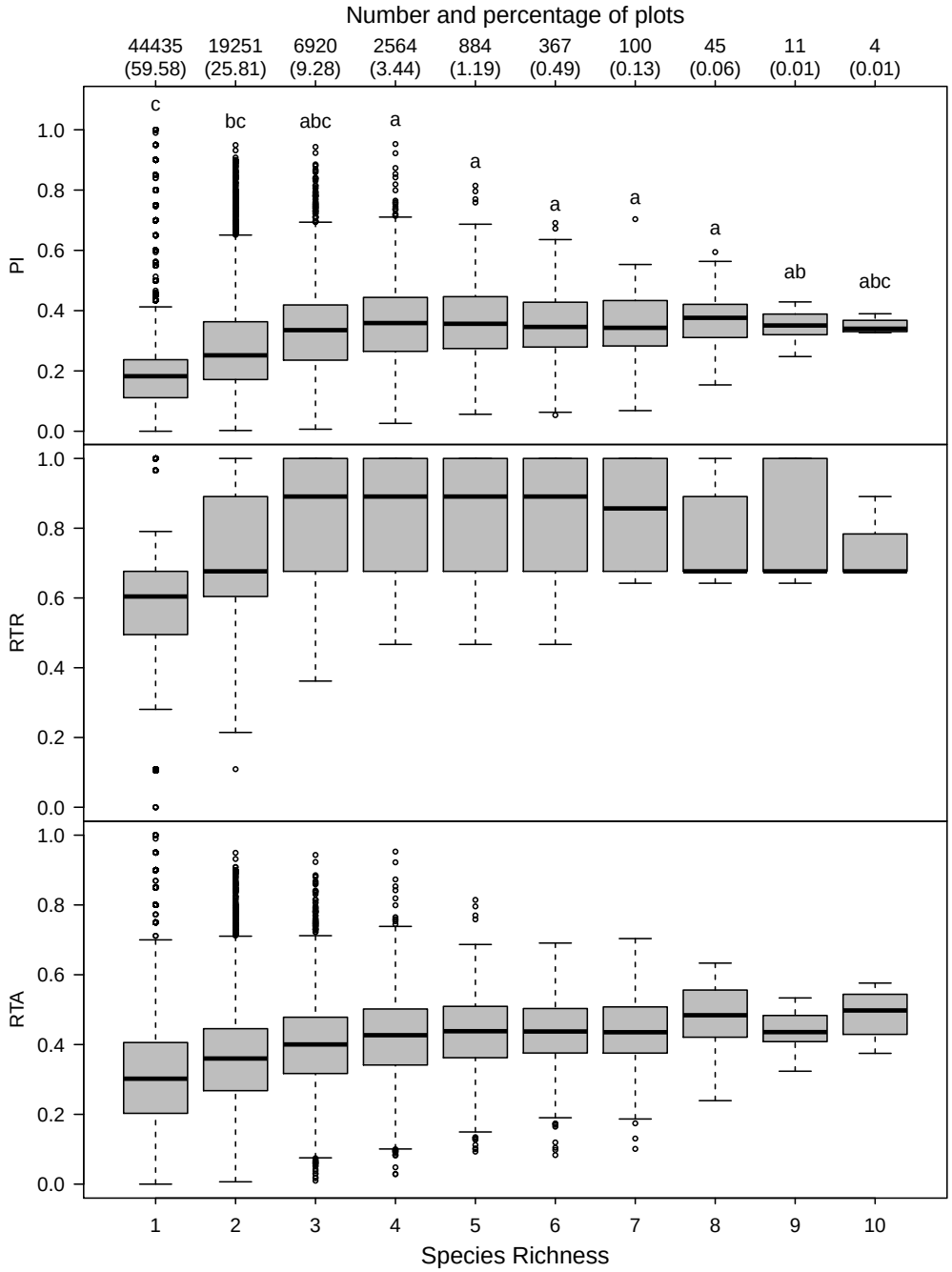

Figure 5: Relationship between tree species richness and PI (top), RTR (centre) and RTA (bottom) values for the 74,581 forest plots in the case study. Black lines in box centres are medians, boxes show interquartile range (25-75%), and whiskers show 1.5 interquartile range. Top axis shows total number and percentage (in brackets) of plots that hold the given number of species. Letters in the top figure are based on Tukey's HSD test.

weighting traits according to the particular biological question at hand is not an easy task and requires a deep understanding of the factors involved (Petchey and Gaston, 2006).

Despite the flexibility and broad scope of the PI, its operational application requires a number of issues to be addressed. Because the Persistence Index is based on trait data, the selection of traits to be included is a crucial step. In agreement with the formulation of PI, results drawn from simulations indicate that its value may change depending on the frequency of the considered traits in the communities under study. Therefore, including a trait that is abundant in the community will cause an increase in PI and vice versa, if the traits are not frequent, PI would decrease (changes in RTR and RTA as a function of trait frequency are shown in Appendix S3.1). Accordingly, it is noteworthy that the results obtained in our case study may be different if other traits or disturbances had been selected. Moreover, results obtained from simulations showed that, while the identity of the traits had a strong effect on PI, the number of traits hardly affected the results of PI, especially when all the traits considered had a similar likelihood of being present in the community (cases A and C). The optimal number of traits to include in the calculation of PI remains thus at the discretion of the user.

Another issue related to trait data might be the potential lack of information on response traits for species that are important to sustained maintenance of the desired ecosystem functions. For instance, despite huge worldwide efforts to compile as much information as possible on plant traits –see for example the LEDA Traitbase (Kleyer et al., 2008), the USDA Plant Compilation (Green, 2009) or the TRY Plants Trait Database (Kattge et al., 2011)– there are still very few databases available on response traits to disturbances, particularly for the Mediterranean Basin and for certain plant species as shrubs (but see Paula and Pausas 2009, Paula et al. 2009, Bagaria et al. 2012). Moreover, ecosystem resilience and resistance to disturbances do not only depend on the variables included in the calculation of PI (Standish et al., 2014). In our particular application to forest communities, a sounder estimation of their vulnerability to disturbances might be attained by combining the information provided by our index with other sources of information, such as environmental and management variables (e.g. accumulation of fuel, size and slenderness of trees, forest structure, silvicultural practices; Herrero and Zamora, 2014; Merlin et al., 2015; Puettmann, 2011).

As expected, the presence of several dominant species in a community implied a higher likelihood of presenting higher diversity and redundancy of response traits (and thus a greater potential persistence). However, both simulations and the case study reflect how the PI increment resulting from adding new species saturates at a given species richness value. In effect, and analogously to the "rivet" model of ecological function (Ehrlich and Ehrlich, 1981), as species are added to an ecosystem, their response traits start to overlap up to a point where any increment in number of species does not involve any great difference in number of response traits present in all species (Reich et al., 2012), in which case the PI will no longer increase at the same rate.

The general low correlations between PI and the most common FD indices were not surprising due to the different concepts they reflect. These differences in concepts and basis make them complementary for their application in the management of ecosystems. While PI is focused on the presence and abundance of response traits in species of the target community, the FD indices are focused not only in the presence and abundance of functional traits, but mostly in their range. The use of FD indices thus allows detecting disturbance impacts on the functional trait structure of communities and, therefore, on the functioning of communities (Mouillot et al., 2013). The Persistence Index, for its part, provides a measure of the capacity of communities to cope with potential disturbances on the basis of their species responses.

4.2 Future perspectives and applications

The PI is flexible enough to be applicable to the study of a wide range of ecological and management-relevant issues. For example, calculating PI at different time-points-such as in successive forest inventories-can provide useful information on temporal variations in the ability of ecosystems to withstand disturbances. This opens the possibility of using this index as an indicator of the consequences that past disturbances or management decisions have had on ecosystems in terms of enhancement (or deterioration) of their persistence and adaptive capacity. At the same time, the index could be used to assess the future consequences of various management or disturbance scenarios using modeling techniques at an appropriate spatial resolution. The continuous assessment of how management affects the adaptive capacity of ecosystems is a cornerstone of some of the proposed methods of environmental management to contend with global change, such as ecosystem-based management or managing for complexity (Gauthier et al., 2008; Messier et al., 2013; Mori et al., 2013b).

Given the importance of thresholds in operationalizing the concepts of resilience and resistance into real-world management (Lake, 2013; Standish et al., 2014), future efforts need to focus on the evaluation of the index, and should aim at finding the minimum value needed to ensure the persistence of specific ecosystem functions in the event of natural disturbances. These could be conducted by comparing the response of a set of communities with similar environmental conditions –but different PI values– to disturbances with comparable severity.

In conclusion, our formulation of PI is a first attempt to quantify the persistence of ecosystems based on the diversity and redundancy of response traits. Additional developments could be implemented and, in the case of its application to forest communities, include consideration of structural diversity, which has been proposed as a key factor determining forest resilience and resistance to disturbances in areas where disturbance agents tend to affect trees of a specific size range (Brang et al., 2014; Lafond et al., 2013; O'Hara and Ramage, 2013). Despite room for improvement, we believe that the current formulation of the Persistence Index offers a general tool for assessing the persistence of a broad spectrum of communities subjected to different types of disturbances. Therefore, not only it can contribute to a better understanding of how ecosystems respond to disturbances, but it can also be a useful tool to guide natural management decisions in a changing and uncertain world.

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